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Short communication

A catch-22 conflict: Access to semi-domestic reindeer modulates Eurasian lynx depredation on domestic sheep

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ABSTRACT

Conserving large carnivores in multi-use landscape is a global challenge. In northern Norway the presence of Eurasian lynx (*Lynx lynx*) conflicts greatly with the current ways of keeping free-grazing, unguarded livestock in large carnivore habitat. In contrast to most other places in Europe, livestock (sheep *Ovis aries*, reindeer *Rangifer tarandus*) are the only ungulate prey available for lynx in this area. The relative preference by lynx for these two domestic species will strongly influence depredation pressure for the respective species. We examined predation patterns on domestic sheep in summer from 17 GPS-collared lynx that had access to both free ranging sheep and reindeer. During 1115 lynx monitoring days, we documented 47 sheep and 274 reindeer killed by lynx. Most lynx individuals selected reindeer over sheep and the probability for a kill to be a sheep increased at low reindeer densities combined with high sheep densities. Kill rates on sheep were several times lower than for reindeer and were not related to density of livestock. General avoidance and low kill rates on sheep by most lynx generated low predation pressure on sheep within the reindeer husbandry, similar to what has been observed in areas of high roe deer densities. However, even a small shift of herd location within the designated summer grazing areas for reindeer could potentially cause a significant increase in depredation on sheep locally. This is one of several studies demonstrating that the density of alternative prey can modulate kill rates on livestock, which is important to include in spatially explicit risk models of large carnivore depredation on livestock.

1. Introduction

The conservation of large carnivores in a multi-use landscape is widely associated with a range of conflicts including depredation on livestock, which is globally recognised as one of the most widespread barriers to increasing public acceptance of carnivores (Baker et al., 2008; Zimmermann et al., 2010). The extent of this conflict varies greatly depending on factors like predator and livestock species identities and densities, body size ratio between carnivore and livestock, landscape characteristics, and wild prey availability (see reviews in Baker et al., 2008, Inskip and Zimmermann, 2009; Zimmermann et al., 2010). Livestock husbandry practices are also often of great importance in modulating predation impacts (Linnell et al., 2012), with free ranging, extensive pastoral systems most exposed. The future of such pastoral systems is currently facing many pressures and there is a global focus on food production, rural development and the conservation of biocultural diversity with associated grazing dependent biodiversity (Maffi and Woodley, 2010). These globalisation processes are influenced by large carnivore depredation because it represents one additional cost to producers (when livestock are killed) and mitigation often requires higher inputs, especially in terms of labour. It is therefore crucial that economic mechanisms be found to either compensate for losses or finance mitigation. However, because of the huge variation in pastoral systems and carnivore livestock conflicts it is necessary to base action on an understanding of the underlying ecology (Linnell et al., 2001b).

The conflicts associated with large carnivore depredation on livestock are especially high in Norway because of the present grazing systems which are based on free-range grazing of unguarded domestic sheep (summer only) and semi-domestic reindeer (all year round) in carnivore habitats (Kaczensky, 1999; Swenson and Andrén, 2005). Seasonal livestock grazing areas cover two thirds of the land area of Norway, and depredation by five large predators (Eurasian lynx *Lynx lynx*, wolverine *Gulo gulo*, brown bear *Ursus arctos*, golden eagle *Aquila chrysaetos* and wolf *Canis lupus*) is widespread (Swenson and Andrén, 2005).

In Norway, there is a legal requirement that all livestock losses to large carnivore depredation should be fully compensated.

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Currently, an *ex post facto* compensation system (Schwerdtner and Grüber, 2007) based on estimated losses is in use. However, there is a large degree of uncertainty concerning both the overall magnitude of depredation and the relative impact of the different predator species, because only a small fraction (4–9%) of the compensated sheep and reindeer are subject to a formal post mortem analyses (www.rovbase.no). Lynx, totalling approximately 400 individuals in Norway, are held responsible for ~30% of the compensated depredation. In 2012 alone, the Norwegian government paid 130 million NOK (15 million euros) in compensation for losses of 26,836 sheep and 19,704 reindeer (www.rovbase.no). Because of the high costs and controversy over the exact magnitude of depredation there is currently a political discussion in Norway concerning a transition to a risk based incentive system like the one currently used in Sweden for reindeer (Zabel and Holm-Müller, 2008). Such systems are believed to encourage depredation prevention rather than damage documentation and reduce transaction costs (Ferraro and Kiss, 2002). For such systems to operate it is essential to have knowledge about carnivore predation patterns on livestock in different environmental settings.

Lynx in Scandinavia prey on a large spectrum of species, from small mammals and birds to wild and domestic ungulates, and display a substantial variation in diet (Odden et al., 2006; Mattisson et al., 2011b; Gervasi et al., 2014). The widespread nature and high densities of domestic prey in Norway creates a predator–prey system that is unlikely to be driven purely by wild prey. In southern Norway depredation rates on sheep are positively influenced (i.e. decreased) by the density of roe deer (Odden et al., 2008, 2013; Gervasi et al., 2014) and in turn, the abundance of sheep influences kill rates on roe deer. In central-Norway, where the distributions of roe deer, domestic sheep and semi-domestic reindeer overlap, lynx prey on all species but show a preference toward roe deer (Moa et al., 2006; Sunde et al., 2000). In northern Norway, where roe deer are functionally absent due to harsh winters (Mysterud et al., 1997), the only ungulate species available for lynx are both livestock (sheep and reindeer), with semi-domestic reindeer representing the main prey of the lynx (Mattisson et al., 2011b). In summer, when sheep are released in forest and alpine tundra pastures after overwintering in barns, lynx locally experiences a superabundance of domestic prey, with densities far greater than observed for wild ungulate species elsewhere in Norway.

In this study we test predictions emerging from our earlier studies in southern Norway, where alternative prey abundance to a large degree modulates lynx depredation patterns on free-ranging sheep (Odden et al., 2008, 2013; Gervasi et al., 2014). To better understand the underlying process of depredation we analyse individual predation patterns in an environment lacking wild ungulates and determine whether this is caused by an active selection process or as a result of different prey abundances. Because semi-domestic reindeer constitute the major dietary item for lynx in this area (Mattisson et al., 2011b) we predict that lynx select reindeer over sheep.

2. Methods

2.1. Study area

The study was conducted in Troms and Finnmark counties (69°00′–70°10′N, 19°90′–25°00′E) in northern Norway. The area is characterised by a coastal alpine climate. Alpine tundra dominates the area followed by mountain birch forest (*Betula pubescens*) and small patches of pine forest (*Pinus sylvestris*) along the coast and in some of the valleys. Human densities are low (2/km^2 in Finnmark and 6/km^2 in Troms). The ungulate community is dominated by largely unattended free-ranging domestic sheep and semi-domestic reindeer. Moose (*Alces alces*) are the only wild ungulate occurring in significant numbers, but are not considered an important prey for lynx because of their large size. Roe deer, the main prey of lynx in southern Scandinavia (Odden et al., 2006) can be regarded as functionally absent, even if a few individuals may occur in low lying coastal areas. Mountain hares (*Lepus timidus*), tetraonids (*Lagopus* spp., *Tetrao* spp.), red foxes (*Vulpes vulpes*), and small rodents (*Clethrionomys* spp., *Microtus* spp. and *Lemmus lemmus*) are alternative prey species for lynx (Mattisson et al., 2011b).

2.2. Lynx capture

Lynx were equipped with GPS-collars after being darted from a helicopter and immobilized with medetomidine-ketamine, following pre-established protocols (Arnemo et al., 2012). We used GPS-collars which transferred data via the GSM network (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). The handling protocols were approved by both the Norwegian animal research ethics committee and wildlife management authority.

2.3. Predation studies

We conducted predation studies on 17 lynx individuals (6 males, 11 females) in the summers from 2008 to 2013 that had access to both sheep and reindeer grazing areas within their home ranges. During periods of intensive monitoring ($\bar{x} = 29$ days duration, range: 19–61 days; hereafter called predation periods), GPS-collars were programmed to take between 7 and 24 locations a day ($\bar{x} = 15$). Kills were found by visiting clusters of lynx GPS-locations and we attempted to investigate all sites with $\geqslant 2$ GPS locations, excluding obvious daybeds (see Mattisson et al., 2011b for further details on method used). All predation periods included in the analyses were conducted between 1st June and 6th September when both reindeer and sheep were available.

2.4. Prey density

Sheep and reindeer graze freely over large parts of Norway and the grazing areas overlap to a large degree (Appendix A). For sheep density we used data from the Norwegian Forest and Landscape Institute (2008–2012, http://www.skogoglandskap.no/), which reports the number of sheep released each year in spring within each grazing district. The average sheep density in the district that overlapped with the lynx (mean size 228 km^2 ± 66 SE) was 19.5 sheep/km^2 (range: 3–98). For reindeer density we used data from the Reindeer Husbandry Administration (2008–2011, http://www.reindrift.no/). The reported number of reindeer in winter (March 1st) for each district each year was added to the reported number of calves born the subsequent summer to determine the total number of reindeer present in summer. Reindeer density was estimate using the official borders of the designated summer grazing areas (mean size 973 km^2 ± 187 SE). The average reindeer density was 14 reindeer/km^2 (range: 4–29). One summer grazing area in Norway was used by a Swedish reindeer district whose reindeer migrate across the border each year. Here we only had data on number of reindeer in winter and no data on number of calves born. To retain summer numbers we assumed the same ratio between summer and winter numbers as the average for the other districts (1.6). As the variation in density among districts was much higher (sheep: $F_{11,61} = 103$, $P < 0.001$; reindeer: $F_{18,72} = 130$, $P < 0.001$) than among years (sheep: $F_{5,61} = 0.6$, $P = 0.7$; reindeer: $F_{4,72} = 1.5$, $P = 0.2$) we used an average density of all years for each district.

The estimated summer densities represent numbers at the beginning of summer (i.e. at the time of release for sheep and after the birth period for reindeer) and do not account for incremental losses over the summer. The spatial resolution of the estimated densities is quite coarse and we had to assume a homogenous prey density inside the grazing areas. These densities should therefore be used as a general index of relative density rather than true densities. There may be a high degree of local variation in time and space within the districts. In addition, both reindeer and sheep may wander outside the designated areas as these are not fenced.

2.5. Analyses

We performed prey selection analyses using two approaches. Firstly, we used each predation period of individual lynx as a sample and calculated the proportion of kills that were sheep among all reindeer and sheep kills during that period. Prey availability was estimated inside a minimum convex polygon (MCP) created from all available lynx GPS-locations of each predation period ($\bar{x} = 399$ locations, ±53SE), buffered with 1 km, thus representing the area used by the lynx during the specific period (average range size for a single period = 569 km^2 ± 70 SE). Prey density within each individual MCP was extracted from overlapping grazing district of respective species using area weighted mean (Geospatial Modelling Environment). Proportion of forest within each MCP was extracted from a $30 * 30$ m vegetation map (Northern Research Institute, Norway).

Secondly, we used each kill site as a sample, being classified as either a sheep or a reindeer. Prey availability was here estimated within 1 km buffer zones around each kill. Although this is not a true local density it does represents the density within the grazing area in which the kill occurred, and provides a higher degree of spatial specificity than the first approach given that all lynx covered multiple grazing units.

2.5.1. Prey selection (1st approach)

Lynx selection of sheep was assessed using Manlys's standardised selection ratio α. α is the probability that sheep are selected when they are available at the same densities as reindeer. $\alpha \approx 0.5$ indicates that lynx use sheep in proportion to availability, $\alpha > 0.5$ indicates selection for sheep while $\alpha < 0.5$ indicates avoidance of sheep (and selection for reindeer).

$$\alpha = (U_S/A_S)/((U_S/A_S) + ((1 - U_S)/(1 - A_S)))$$

where U_S is the relative proportion of sheep kills among lynx killed sheep and reindeer and A_S the relative availability of sheep given by the total sheep and reindeer densities within the lynx MCP (individuals/km^2). α was estimated separately for each predation period.

2.5.2. Prey selection (2nd approach)

To test the influence of local prey densities on lynx prey selection in summer we used binomial generalised linear mixed-effects models in R (R Development Core Team 2008), using the package *lme4* (Bates et al., 2011). As some individuals were followed for more than one summer and thus had multiple predation periods, we fitted mixed-effect logistic regression models with individual lynx as a random effect, to account for pseudo-replication. We used the density of each of the two prey species as explanatory variables. We applied a square root transformation to prey density prior to the analysis to remove the impact of outliers, especially in sheep (with some outliers 3–4 times higher than the average density). For 43 reindeer- and 3 sheep kills (of the 321 kills included in the 1st approach), the buffer zones did not overlap with grazing districts of the respectively species. As the grazing areas are unfenced, animals will occasional stray outside designated areas. These kills were excluded in this analysis.

Several reindeer kills did not overlap any sheep grazing areas, thus to handle the excessive zeros in the explanatory variable "sheep density" we created a binary variable indicating sheep presence/absence. This was included in all models with sheep density using $y = \beta_0 + \beta_1$ (no sheep) + β_2 (sheep density). This gives $y = \beta_0 + \beta_1$ when no sheep are present and $y = \beta_0 + \beta_2$ when sheep are present.

We tested for differences in prey selection patterns (both approaches) among lynx sex (M, F) and categories: males (M), solitary females (F), and females with kittens (Family).

3. Results

During 39 separate predation periods, totalling 1115 lynx monitoring days, we found 274 reindeer kills and 47 sheep kills. In addition, the lynx killed 35 hares, 16 ptarmigans, 7 red fox, 6 black grouse, 10 small birds or mammals, and 1 moose calf. Only nine of the 17 lynx preyed on sheep (53%) whereas all lynx preyed on reindeer. Nineteen of the 39 predation periods included at least one killed sheep (49%) while 35 included at least one reindeer (90%). Two periods included only small prey (5%). Only two periods included sheep but no reindeer kills. Overall mean kill rate on sheep was 1.2 sheep/30 days (±0.25 SE) compared to 7.1 reindeer/30 days (±0.88 SE). There were no significant differences in sheep kill rates among lynx categories (Anova: $F_{2,36} = 1.2$, $P = 0.3$). Variation in sheep kill rates was not explained by either density of sheep or reindeer (Fig. 1). While reindeer kill rates was unaffected by the density of sheep, they correlated positively with reindeer density (Fig. 1). Lynx-killed sheep were mainly found in the forest (74%) while reindeer kills were equally found in the forest (51%) and on the tundra (49%). Mean proportion of forest within the range used by the lynx was 38% (±16 SD).

3.1. Prey selection (1st approach)

In general, lynx avoided sheep (mean $\alpha = 0.24$, ±0.05 SE) although there was some variation among lynx categories (Fig. 2; Anova: $F_{2,34} = 3.4$, $P = 0.047$). Males showed stronger avoidance for sheep than females with and without kittens (males: $\alpha = 0.093$, ±0.04 SE; family: $\alpha = 0.32$, ±0.12; females $\alpha = 0.39$, ±0.12 SE). Assuming weak or no selection when α is between 0.4 and 0.6, only six predation sequences showed selection for sheep. These exclusively consisted of female lynx (15%, Fig. 2a). Nine lynx individuals were studied during at least two different periods. Among them, three individuals always avoided sheep ($\alpha < 0.4$), while one always selected for sheep ($\alpha > 0.6$; Fig. 2b). There were no correlation between the relative use of sheep by lynx and relative sheep density ($r^2 = 0.005$, $t_{35} = 0.9$, $P = 0.4$).

Within the range used by the lynx during the predation periods, average prey density was 8.2 sheep/km^2 (±4.9 SD) and 11.6 reindeer/km^2 (±4.9 SD) and there were no correlation between sheep and reindeer density ($r^2 = 0.02$, $P = 0.8$).

3.2. Prey selection (2nd approach)

The probability of a lynx kill to be a sheep was negatively influenced by reindeer density ($\beta = -1.9$, SE = 0.63, $P = 0.002$) and positively influence by sheep densities ($\beta = 0.7$, SE = 0.23, $P = 0.001$) following the best supported model in the logistic regression analysis (Table 1 and Fig. 3). The inclusion of lynx sex improved the model, showing a small increased in proportion of sheep kills for female lynx. However, the probability for a kill to be a sheep rather than a reindeer was in general low across all prey densities, only starting to show a preference for sheep at a combination of low reindeer densities and very high sheep densities. All models including sex (M, F) instead of lynx category (males, solitary female, females with kittens) performed better (ΔAIC = 2), thus only sex was retained in the presentation. In addition, there was

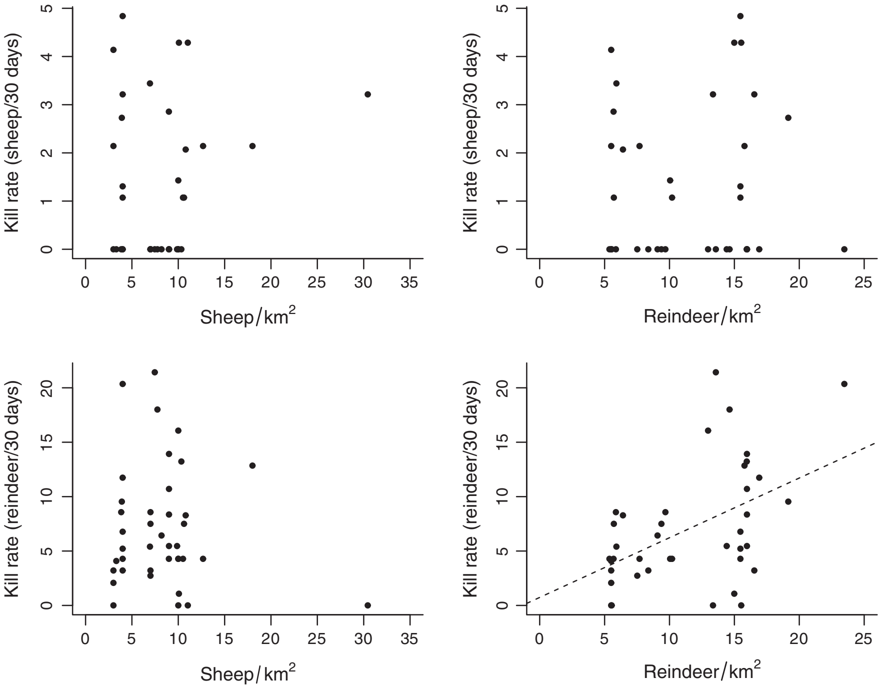

Fig. 1. Relationship between lynx kill rates on sheep and reindeer (individuals killed per 30 days) and prey density within the lynx range. The relationships were not significantly different from zero except for reindeer kill rate and reindeer density ($r^2 = 0.2$, $P = 0.002$, $n = 39$).

a high variance in the random intercept between individuals (7.5, 2.7 SD).

Mean prey density around all kills was 5.1 sheep/km^2 (±11.9 SD) and 13.6 reindeer/km^2 (±5.7 SD) which increased to 15.4 sheep/km^2 (±26.0 SD) and decreased to 9.9 reindeer/km^2 (±6.5 SD) around sheep kills.

4. Discussion

Even though northern Norway is relatively sparsely populated, the presence of carnivores still has an impact on humans as it conflicts with the ways of keeping livestock; free ranging and largely unattended in extensive areas of natural carnivore habitat (Kaczensky, 1999). In contrast to most other places in Europe (Jobin et al., 2000; Stahl et al., 2001; Odden et al., 2006), livestock is the main prey for lynx in this area (Mattisson et al., 2011b). However, lynx did not predate opportunistically on livestock; reindeer were clearly selected over sheep although we observed a degree of individual variation, common in lynx and carnivores in general (Mattisson et al., 2011b; Elbroch and Wittmer, 2013a; Gervasi et al., 2014). The probability of killing sheep was inversely related to reindeer density which is in agreement with the results from our previous work in southern Norway where the predation pattern on sheep was highly influenced by densities of wild ungulate prey (Odden et al., 2013; Gervasi et al., 2014). Lynx kill rates on sheep was consequently low in the reindeer husbandry area (1.2 sheep/30 days), similar to kill rates observed in areas with high roe deer densities in southern Norway (1.1. sheep/30 days; Odden et al., 2013). In contrast, summer kill rates on reindeer were much higher (7.1 reindeer/30 days) than observed on wild ungulates in Norway (1.3–5 roe deer /30 days; Nilsen et al., 2009; Gervasi et al., 2014). This may partly be explained by high prey densities and by increased competition with scavengers on open tundra (Mattisson et al., 2011a), a phenomena also observed for other carnivores (Kaczensky et al., 2005; Krofel et al., 2012; Elbroch and Wittmer 2013b).

The general avoidance and the low kill rates of sheep by most lynx individuals are likely to generate a low predation pressure on sheep in areas with reindeer; similar to areas of high roe deer densities (Odden et al., 2013; Gervasi et al., 2014). As the lynx population in Norway is under high harvest pressure (Linnell et al., 2010; Nilsen et al., 2012) and thus prevented from displaying a numerical response to increasing prey abundance, we do not expect an increased predation pressure on the selected reindeer in the presence of sheep. In addition, reindeer densities in the study area are very high during the time when sheep are present and there is little evidence that sheep abundance influences predation on reindeer.

Our results indicate that depredation on sheep by lynx in the reindeer husbandry area occurs mainly when lynx are in areas of high sheep density. High densities of sheep seem to generate a certain degree of depredation on sheep by lynx across all of Norway (Odden et al., 2002, 2006). But the relatively low kill rates on sheep compared to reindeer suggest little active preferences for these areas as the range use of the lynx favoured higher densities of reindeer (sheep/reindeer density < 1, Fig. 2a). Although lynx spend significant time also on the tundra they do select for forested habitat (Rauset et al., 2013), a habitat in which the majority of sheep kills were found. This is consistent with previous findings that foraging patch selection in Eurasian lynx is determined by the abundance of natural prey species, rather than the availability of livestock (Moa et al., 2006; Odden et al., 2008).

Selection for sheep was more common among female lynx but we observed no differences in sheep kill-rate among lynx sexes. This contrasts with studies from southern Norway where males were responsible for most of the depredation on sheep (Odden et al., 2002; Linnell et al., 1999), although they did not select more for sheep than females with kittens (Gervasi et al., 2014). Males use larger areas than females (Linnell et al., 2001a; Mattisson et al., 2011c) and move greater distance (Mattisson et al., 2010) thus predation by males may be more random and depend more on local encounter rate than female predation. The selection for sheep by a few lynx individuals may rather be explained by individual

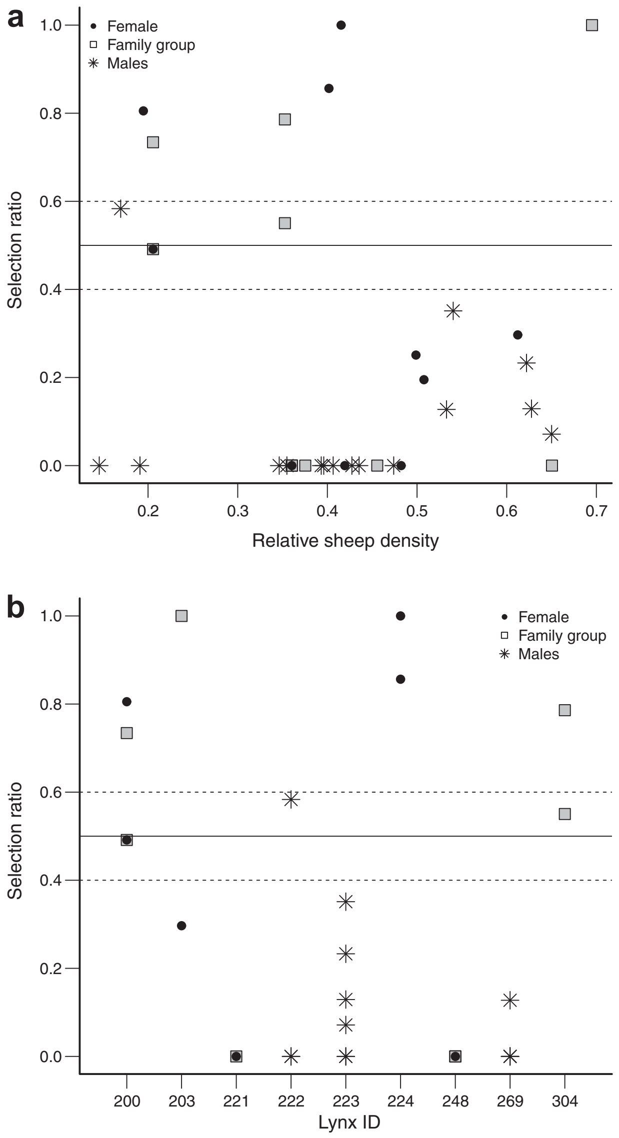

Fig. 2. Manly's selection ratio (α) for sheep by lynx [0 = only reindeer kills, 1 = only sheep kills] in relation to (a) relative sheep density [0 = only reindeer, 1 = only sheep] and (b) individual variation among nine lynx with at least two separate predation periods. Alpha values above 0.5 suggest selection for sheep while values below suggest selection against. When sheep density > reindeer density (a: $x > 0.5$), lynx will occasionally kill sheep (a: $y > 0$) but still not select for them. Selection for sheep is primarily seen at lower relative sheep density (a: $x < 0.5$) and only by female lynx and family groups ($a + b$).

Table 1
Model selection for binomial GLM analysis of prey selection (sheep/reindeer) by lynx in northern Norway 2008–2013 based on 275 kills.

Model	d.f.	AIC	ΔAIC	Weight
Reindeer + sheep[a] + lynx sex[b]	6	109.5	0.00	0.60
Reindeer + sheep	5	110.3	0.80	0.40
Sheep + lynx sex	5	132.8	23.3	0.00
Sheep	4	132.9	23.4	0.00
Reindeer + lynx sex	4	173.1	63.6	0.00
Reindeer	3	174.4	64.9	0.00
Lynx sex	3	197.4	87.8	0.00
Null	2	198.0	88.5	0.00

[a] The term "Sheep" includes two variables; one binary (presence (0)/absence of sheep (1)) and one continuous for sheep density.

[b] Lynx sex (M, F) always performed better than lynx sex * status (M, F, F with kitten) thus sex * status were not included in final model selection.

preferences (Elbroch and Wittmer, 2013a; Gervasi et al., 2014) than sex, but may also be driven by a finer scale prey density or vulnerability than we were able to measure.

A consequence of domestication is reduced anti-predator behaviour (Reimers et al., 2012), and as sheep are kept inside barns in winter (while reindeer are free ranging year around and only handled a few times a year) sheep were expected to be an easier prey for the lynx than the reindeer. Encounter rate with sheep is also expected to be higher as sheep breeds in Norway do not tend to aggregate, while reindeer are often found in large groups. So why do lynx show a preference for reindeer? As both species are free-ranging and largely unattended during summer, it cannot be explained by differences in human presence or activity. Prey body size is neither a good explanation as sheep and reindeer are of similar size. We can only speculate that reindeer are perceived by the lynx as being closer to their wild cervid ancestors than sheep, and lynx seem to have a preference for wild prey (Stahl et al., 2001; Odden et al., 2002; Moa et al., 2006; Odden et al., 2013; Gervasi et al., 2014). In addition, the wool of the sheep is thick and impregnated in lanolin and may have a deterrent effect on the lynx.

5. Implications for management

Unwanted effects of management actions are not uncommon (Wittmer et al., 2013) and any information that can help prevent this is essential. This study confirmed our earlier findings that lynx will inevitably kill sheep at some stage as long as unguarded sheep are found at high densities throughout the natural habitats exploited by lynx. Any mitigation strategy (such as fencing) that reduces the number of encounters between lynx and sheep will reduce the depredation rates observed. However, in areas where all large prey species are livestock, depredation will be a trade-off between losses of different species of livestock. Thus preventing depredation on one livestock species may directly increase depredation on a second species or the relative densities may influence depredation pressure for both species. If changes in husbandry could reduce lynx access to sheep our results show that the risks of any significantly changes in predation on reindeer are very small. In contrast, a sudden absence of reindeer is likely to have a significant influence on sheep depredation, at least temporally until the lynx population responded negatively to the total lack of ungulate prey in winter. Even a small shift of reindeer locations within the designated summer grazing areas could potentially cause a significant increase in depredation on sheep locally.

The present day Norwegian ex post facto compensation system creates widespread social conflicts because only a small fraction of the compensated sheep losses are documented despite the investment of considerable effort in searching for and inspecting kills. Before an eventual introduction of a national risk based incentive system (Zabel and Holm-Müller, 2008), which is believed to encourage depredation prevention rather than damage documentation, it is important to predict the risk of sheep depredation by lynx nationwide as accurately as possible (c.f. Herfindal et al., 2011). As it has been shown that the density of other ungulate prey, both wild species and domestic reindeer can modulate sheep kill rates (this study for reindeer; Gervasi et al., 2014 and Odden et al., 2013 for roe deer) it is important that these parameters are included in an eventual spatially explicit risk model of sheep depredation to get a more accurate estimate. In addition, we observed a high degree of individual variation in prey preference unexplained by sex or prey abundance, including complete avoidance of sheep by some individuals. Although hard to predict, this is nevertheless essential to keep in mind when implementing models on predator–prey dynamics as it can have great consequences on the outcomes (Pettorelli et al., 2011; Wittmer et al., 2014). This

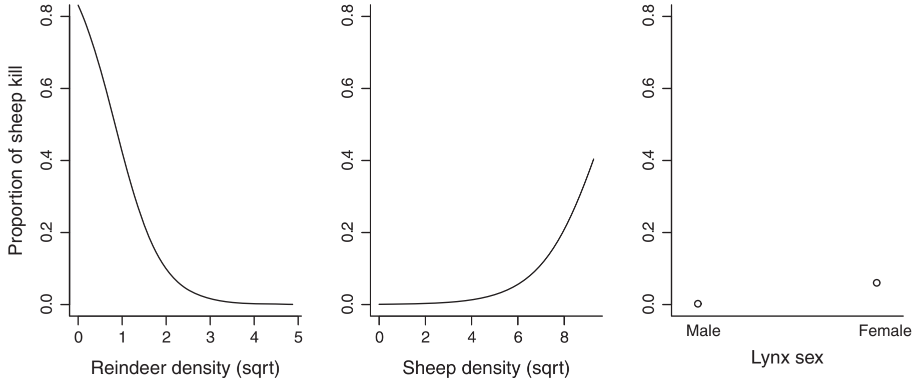

Fig. 3. Plots of each predictor of the proportion of sheep killed by lynx based on the most supported model (Table 1). Other factors in the model are kept at the reference level and numerical predictors are adjusted for with the median value. Both prey densities (individual/km^2) are squared root.

approach initially requires a large amount of ecological data, but opens the way to an economic mechanism that can help share the costs associated with large carnivore depredation in a manner which is fair, transparent, efficient and that stimulates better husbandry and hopefully a more viable pastoral system that can accommodate the presence of predators.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.09.004.

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